

# THE MUSCULAR ACTIVITY AND OXYGEN CONSUMPTION OF URECHIS CAUPO

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## I. INTRODUCTION: NATURAL HISTORY

*Urechis caupo*, a large marine echiuroid worm recently discovered on the California coast by Fisher and MacGinitie (1928), presents by virtue of its habits of life a unique opportunity for the quantitative study of the interrelations between muscular activity, rate of metabolism and the mechanism of exchange with the environment.

The animal digs and lives in a U-shaped burrow in the mud of shallow estuaries, leaving it only occasionally to construct a new burrow. The upper ends of the burrow open freely to the water. The requisite exchanges with the environment: respiratory, nutritive, excretory and reproductive, are accomplished by the animal forcing a stream of water through the burrow. The movement of water is produced by peristaltic waves in the musculature of the body wall, originating at or near the anterior end, and passing posteriorly. The integument in the region between two consecutive waves is pressed closely against the wall of the tube. Accordingly, water between the integument of the constricted regions and the sides of the burrow is carried posteriorly with the peristaltic wave. The worm from time to time turns around in the tube, thus reversing the direction of the stream.

The mode of feeding is unusual. Near the anterior end of the worm there is a ring of specialized mucous glands. The animal presses the body wall in the region of these glands firmly against the side of the burrow; then, as the glands secrete, it backs away, leaving a tube of mucus attached to the burrow at one end, and to its integument at the other. The peristaltic movements, usually suspended during the formation of the tube, are now resumed, drawing a stream of water through the mucus tube, which acts as a filter. Particles over one micron in diameter are retained. After filtration of water has continued for some time, the worm moves forward, seizes the tube with the proboscis and swallows it whole. Since the food consists of particles included in the detritus of the estuary bottom, this mechanism enables the animal

to obtain nutriment without leaving the burrow. The above description of the animal's habits is adapted from Fisher and MacGinitie's account.

*Urechis* may be kept in the laboratory indefinitely if placed in glass U-tubes of dimensions approximating those of the burrow and if given access to aerated sea water. Several specimens, introduced into such tubes over three years ago by Professor MacGinitie of the Hopkins Marine Station, are now in excellent condition. Their behavior in the laboratory is consistent, as far as is known, with that in their natural habitat.

## II. ACTIVITY: VOLUME OF WATER PUMPED THROUGH TUBE

The volume of water pumped through the tube in which the animal is living is of interest from two viewpoints: First, since the peristaltic activity of the body wall musculature constitutes by far the greatest part of the muscular activity of the animal, a measure of the volume pumped may be regarded as an approximate indirect measure of the total muscular work. Second, since all exchanges with the environment are mediated through this stream, its measurement yields data relative to the potentially available oxygen and food supplies, and to the facilities for disposal of metabolites and reproductive products.

The method of measurement of the volume pumped is closely related to that devised by Galtsoff (1928) for the study of the flow of water produced by the gills of the oyster.

The apparatus is diagrammed in Fig. 1. One *Urechis* (*A*) was introduced into a glass U-tube (*B*), about 2.5 cm. in diameter, the length of the horizontal segment being 30 cm. and that of each vertical segment 25 centimeters. The tube was placed in an aquarium of approximately 100 liters capacity, through the glass front of which the animal could readily be observed. A stream (*J*) of aerated sea water, filtered free of food materials, entered the aquarium continuously and overflowed from a fixed aperture (*C*), thus maintaining a constant level in the aquarium. The temperature in the aquarium ranged from 15.4 to 18.8° C., the average being 16.9 degrees.

The ends of the U-tube projected above the level of the water in the aquarium. A siphon tube (*D*) admitted water from the aquarium into the artificial burrow at one end. The water, forced through the tube by the work of the worm, passed by means of a second siphon at the other end into an Erlenmeyer suction flask (*E*). The flask was so adjusted that, when filled until water overflowed through the side tube (*F*), the level in the flask was the same as that in the aquarium. Since the level of water in all vessels was the same, the only factor causing water to move was the pumping activity of the worm. The

overflowing water was caught in a graduated cylinder (*G*). Collections were made, as a rule, for five-minute periods. The rate of flow was expressed in cubic centimeters per minute.

Since the animals frequently turn around in the tubes, it was necessary to duplicate inlet siphon, outlet siphon and overflow flask, so that the flow could be measured in either direction. The siphons not necessary at the moment were closed with pinchcocks. For simplicity, there is represented in Fig. 1 only that portion of the apparatus required for measurement of the flow in a single direction.

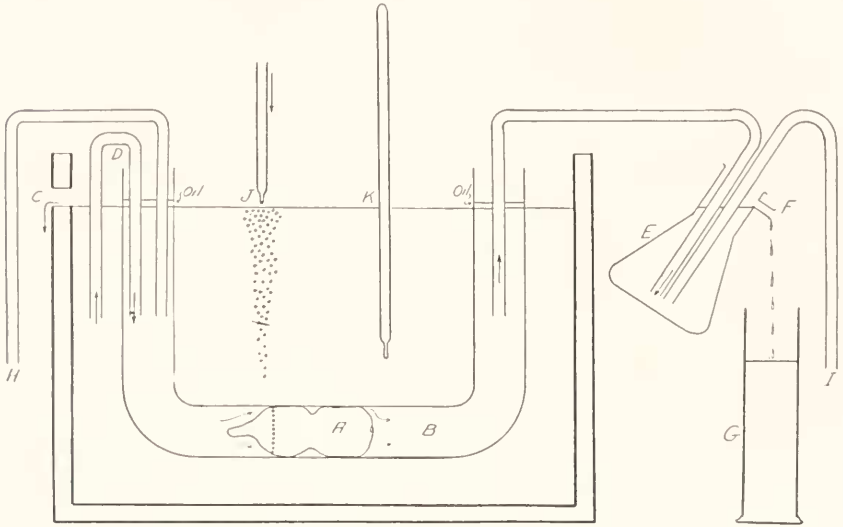


FIG. 1. Apparatus for measurement of volume of water pumped by *Urechis*. Description in text.

The high degree of variability in the rate of pumping which was found made it seem wise to make a number of observations on a few individuals over a considerable period of time rather than a few observations on each of a large number. Accordingly, only two animals were employed, both near the average size of mature worms, *i.e.*, about 60 grams weight. Worm I was perhaps twenty per cent larger than Worm II.<sup>1</sup>

<sup>1</sup> Professor G. E. MacGinitie of the Hopkins Marine Station, Stanford University, kindly provided me with the following weights of ten mature specimens of *Urechis*:

	Average, grams	Maximum, grams	Minimum, grams
Total body weight.....	62.5	82.4	35.1
Weight without blood.....	40.7	53.1	21.1
Weight of blood.....	21.8	31.3	12.5

The worms were kept in their tubes undisturbed throughout the whole duration of the experiments,—about two months. A period of about a week was permitted for adaptation to their new environment before collection of data was begun.

### *Results*

With the animals under constant standard conditions, the rate of pumping during five-minute periods ranged from 0 to 50 cc. per minute. Two factors in the production of this variability were noted: (1) a consistent increase during the feeding periods—a factor which has been studied in some detail; and (2) long periods of inactivity during which the worm lies in a cylindrical form with integument in contact with the glass over its whole length and shows no movement. Such periods may last from twenty minutes to well over an hour. They are usually terminated by the worm turning around, and then resuming pumping. Concerning the significance of these periods of inactivity no suggestions are offered.

However, even if these sources of variability be excluded by the choice of non-feeding periods during which the worm was continually active, there remains a high unexplained variability. For example, in the case of Worm I in twelve consecutive five-minute periods, in all of which it was active and during which no feeding occurred, the rate of pumping ranged from 8.3 to 29.2 cc. per minute, the mean being 19.3 and the average deviation from the mean, 5.0 cc. per minute.

### *Average Volumes Pumped*

In Table I the results of a number of experiments are tabulated. The first three columns contain the data for the whole period of each observation; the second three columns, the data for the portion of the period during which the worm was feeding; and the third three columns, the data for the portion during which it was not feeding. The last column shows the ratio of the rate of pumping when the worm was feeding to that when it was not feeding. The averages are weighted.

It will be seen that the larger worm averaged throughout the experiments 16.5 cc. per minute; the smaller, 10.2 cc. per minute. The variability among the averages of the experiments is considerable.

TABLE I  
*Volume of Water Pumped by Urechis under Standard Conditions*

Experiment	Total			Feeding			Non-feeding			Ratio Feeding Non-feeding
	Vol. cc.	Time min.	Rate cc./min.	Vol. cc.	Time min.	Rate cc./min.	Vol. cc.	Time min.	Rate cc./min.	
Worm I	1	2293	138	—	—	—	2293	138	16.6	—
	2	2770	149	18.5	16	31.7	2246	132	16.9	1.88
	3	4529	438	10.3	—	—	4529	438	10.3	—
	4	4435	185	24.0	54	34.4	2579	131	19.7	1.75
	5	3164	129	24.5	37	35.9	1817	91	19.9	1.80
	Average rates			—			—			1.81
	Average rates			16.5			36.5			14.5
Worm II	1	2556	150	17.0	58	25.2	1092	92	11.9	2.12
	2	1599	124	12.9	22	23.1	1089	102	10.6	2.18
	3	2054	444	4.6	32	12.5	1647	412	4.0	3.12
	4	3034	186	16.3	71	23.3	1383	115	12.0	1.94
	Average rates			10.2			22.0			7.2
	Average rates			10.2			22.0			2.35

*Feeding Cycles*

The following descriptive data were obtained from a series of twenty-five cycles during which the worms were observed to be feeding.

*Frequency of occurrence:* Worm I produced a tube on the average 0.7 times per hour; Worm II, 1.5 times per hour.

*Duration of feeding periods,* from completion of tube to swallowing of tube: averages, Worm I 18.3 minutes; Worm II 8.7 minutes. It is interesting to note that the number of minutes spent in feeding per hour of elapsed time is closely similar in the two animals: Worm I 12.8 minutes per hour; Worm II 13.1 minutes per hour. The larger worm, which fed much less frequently, compensated by greater duration of each feeding period.

*Course of activity during the feeding period: Onset:* In 18 of the 25 cycles examined there was a decrease in the volume pumped during the five-minute period during which the tube was formed. The actual

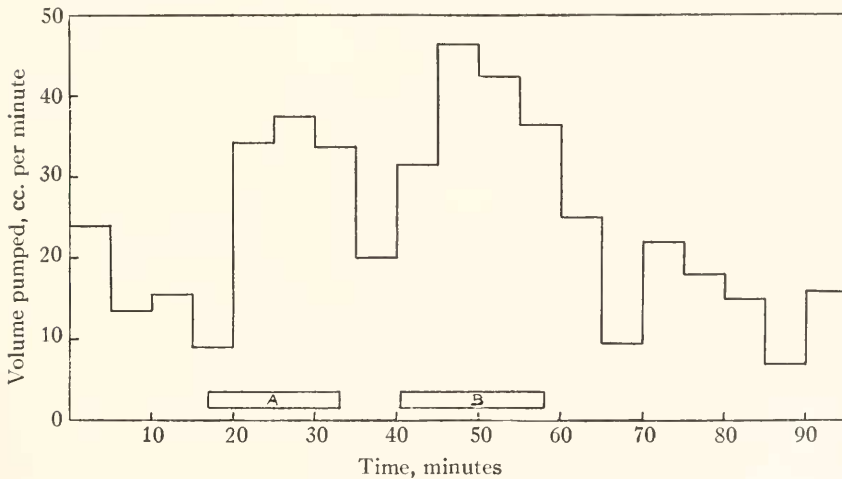


FIG. 2. Rate of pumping by Worm I for a 95-minute period, during which two feeding cycles occurred. The rectangles A and B indicate the time between the formation and swallowing of the tube in each cycle.

formation of the tube occupied about 30 seconds—during which time active pumping was suspended. *Course:* In the period during which the tube is present, there was observed in 23 of 25 cycles a clear-cut increase in the rate of pumping as compared with the rate before and after the feeding period. There is often a step-wise increase during the first two or three five-minute periods to an irregular plateau in the curve of pumping rate. *End:* Immediately or within five minutes after the swallowing of the tube there is commonly, but by no means in-

variably, a decrease in the rate of pumping to below 5 cc. per minute. In Fig. 2 there are represented graphically two consecutive cycles which occurred relatively closely together.

*Average of activity during the cycle as compared with that during intervals between cycles:* These data are included in Table I. The marked increase during feeding is clearly evidenced by the fact that the average ratio of the rate of pumping during feeding periods to that during non-feeding periods is, in Worm I 1.8; in Worm II 2.3. Comparable increases are present in all experiments without exception. In only two of the 25 cycles examined was there no increase. In one of these periods the worm ate the tube within half a minute of making it. In the other, an increase in activity occurred before the feeding was observed. Here it is possible that the tube had been formed earlier and was overlooked for some minutes.

#### *Discussion*

Since the current of water pumped through the burrow finds its significance to the organism by making possible exchanges of materials with the external environment, a discussion of its rôle with respect to certain of such materials is pertinent.

(1) *Oxygen.* The respiratory significance of the current has been discussed by Redfield and Florkin (1931), their discussion being based in part upon the results communicated in this paper. These authors point out that the animal utilizes only one-third of the oxygen in the water inhaled into the hind-gut. Accordingly, at the normal rate of oxygen consumption 0.013 cc. per minute, a hind-gut ventilation of 6.9 cc. of water would be necessary. Since the average rate of pumping amounts to about thirteen cubic centimeters per minute, the current is about twice that necessary for the maintenance of normal respiratory relations.

In an attempt to determine the mechanism of adaptation of the worm to waters of low oxygen content, in eight experiments conducted with the apparatus described above, the worms were given access for approximately an hour to sea water boiled until its oxygen content was reduced from about 4.6 to about 2.5 cc. per liter. The oxygen pressure was thus reduced to about seventy millimeters Hg. The p<sub>H</sub> of the sea water, increased by the boiling, was readjusted to the normal value of 8.2 by addition of a small quantity of dilute hydrochloric acid. The activity of the worms under these conditions was compared with that during similar hour periods, immediately before and after, during which normal sea water entered the tube. No consistent effect was observed,

activity being greater in four experiments, unaltered in one and decreased in three. The average, however, is 40 per cent greater than that of the control periods.

As will be described in Part III of this paper, a reduction of oxygen pressure to 70 mm. Hg is accompanied by a reduction of oxygen consumption to about fifty-five per cent of that in normal sea water. The fall in oxygen consumption is of itself adequate to compensate for the decreased amount of oxygen available in the water. This fact, rather than a consistent increase in the current of water pumped through the burrow, appears to be the adaptive response of the animal to water of low oxygen content. For further discussion of this matter, see Redfield and Florkin (1931).

(2) *Food*. The food requirement of the animal (expressed in some such units as calories per hour), together with the food value of the sea water (in calories per liter), determine the volume of water (liters) which would be required to be filtered in order to meet the requirement. It is conceivable that this might be accomplished by means of a continuous stream of constant intensity. However, *Urechis* instead employs the same device as the higher animals, that of periods of intense food-getting activity alternating with periods in which the animal is freed for other activities. Thus, *Urechis* spends only about one-fifth of its time in the obtaining of food. In order to accomplish the required filtration within this restricted time, a relatively high degree of activity is necessary. Unfortunately the data are not available which would make possible an assessment of the significance of the magnitude of the stream for feeding as has been done for oxygen.

Under the conditions of the experiments the worms were provided with sea water so filtered as to be practically devoid of food value. They had been, and were, accordingly, in a state of chronic starvation. Whether this would serve to evoke a maximum intensity of food-getting activities, or would rather, after a time, cause decreased activity and reduced rate of metabolism as occurs in the chronic inanition of mammals (Lusk, 1928), is not known. However, the fact should be borne in mind in any attempt to apply the data to *Urechis* in its normal habitat.

The stimulus provoking the feeding reaction is not known. That it is not of external origin is shown by the fact that the two worms, in similar tubes side by side in the aquarium, subjected to the same environmental influences, including light, jarring, etc., and receiving the same sea water, carried out their feeding reactions totally independently of each other in time. The stimulus is probably of internal origin.

If, during the period of feeding, a relatively minor mechanical



disturbance be brought about, such as gently moving the inlet siphon tube, the worm abruptly stops pumping, casts loose the mucus tube and backs down into the horizontal part of the U-tube.

### III. OXYGEN CONSUMPTION

The oxygen consumption of *Urechis* was determined by two methods which yielded similar results: (1) a worm, active in a U-tube under the conditions described above, pumped water from the aquarium into the Erlenmeyer suction flask which had previously been filled with mineral oil, so displacing the oil with water. The oxygen content of the water in the U-tube in front of the worm (incoming water) and of that in the flask at the end of the period (outgoing water) was determined by the method of Winkler (1888), samples being withdrawn by means of siphons (*H* and *I* of Fig. 1) without disturbing the animal in any way. Knowing the oxygen content of the incoming and outgoing waters and the volume pumped, the oxygen consumption could be readily calculated.

(2) A worm was placed in a jar containing approximately three liters of sea water, over the surface of which a layer of mineral oil about one-fourth inch thick was floated. Samples of water were withdrawn at intervals by means of a siphon and their oxygen content determined by the Winkler method.

#### *Results: First Method*

In Table II are tabulated the oxygen consumption (in cc. per minute), the oxygen partial pressure in the incoming water (mm. Hg), the oxygen content of the incoming and of the outgoing waters (cc. per liter), and activity or volume of water pumped (cc. per minute). The experiments are arranged in order of increasing activity. It will be noted that there is a general tendency for the oxygen consumption to increase with increasing activity, as would be expected. There is, in these experiments, no consistent relation between the oxygen partial pressure of the incoming water and the oxygen consumption of the animals. The oxygen consumption rate of the two worms is almost identical, being 0.0130 and 0.0136 cc. per minute respectively.

#### *Second Method*

The oxygen consumption of the animals kept in jars under oil was, during the initial period of each experiment, as follows: 0.0141, 0.0173, 0.0281 and 0.0120; average, 0.0179 cc. per minute. These values are definitely higher than those obtained for the oxygen consumption of

worms in the U-tubes. The difference is attributable to the exaggerated peristaltic activity exhibited by the animals in the jars. Apparently, the absence of the normal contact of the integument serves to activate the animal's movements. These values are accordingly considered less representative of the metabolic rate under normal conditions than those obtained by the U-tube method.

A comparison of the oxygen consumption of *Urechis* with that of closely related forms determined by other workers follows.

TABLE II  
*Oxygen Consumption of Urechis in U-tubes*

Animal	Oxygen Consumption	Incoming water		Outgoing water	Activity
		Oxygen Partial Pressure	Oxygen Content	Oxygen Content	
I.	<i>cc./min.</i>	<i>mm./Hg</i>	<i>cc./liter</i>	<i>cc./liter</i>	<i>cc./min.</i>
	0.0091	138.2	4.90	2.80	4.3
	0.0085	127.2	4.51	3.51	8.5
	0.0154	130.0	4.61	3.17	10.7
	0.0123	191.8	6.80	6.10	19.5
	0.0150	93.3	3.31	3.01	50.0
	0.0178	94.2	3.34	3.02	54.3
Average . . . . .	0.0130				
II.	0.0097	133.7	4.74	4.18	17.9
	0.0118	96.0	3.40	2.92	24.7
	0.0194	96.2	3.41	2.92	45.2
Average . . . . .	0.0136				

*Comparison of Metabolic Rates of Certain Invertebrates*

Animal	Author	Oxygen Consumption <i>cc. O<sub>2</sub> gm./min.</i>
<i>Lumbricus</i>	Averaged results of Thunberg, Lesser and Konopacki, quoted by Krogh (1916) . . . . .	0.00189
<i>Glycera siphonostoma</i>	Cohnheim (1911-12) . . . . .	0.00123
	Montuori (1913) . . . . .	0.00025
<i>Hirudo</i>	Rogers (1927) . . . . .	0.00052
<i>Sipunculus nudus</i>	Cohnheim (1911-12) . . . . .	0.00082
<i>Urechis</i>	Present author . . . . .	0.00021

*Urechis* thus possesses a metabolic rate of magnitude comparable to related forms but distinctly lower. This is in part attributable to the fact that this animal has a blood volume disproportionately great for its size as compared with allied forms. Thus, an average-sized

animal weighing 62.5 grams possesses blood weighing 21.8 grams. Although the corpuscles are true cells, it is doubtful whether their metabolism would give to the blood a rate of oxygen consumption per gram comparable to that of the fixed tissues. If the total oxygen consumption be calculated on a basis of fixed tissue weight, it becomes 0.00033 cc. per gram per minute.

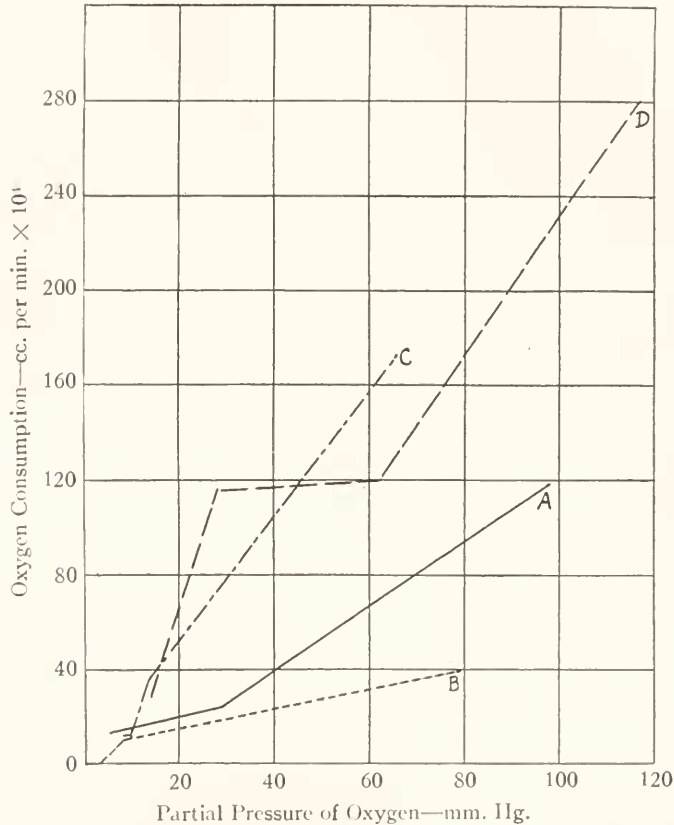


FIG. 3. Relation of oxygen consumption to oxygen partial pressure. *Urechis*. The letters at the extremities of the curves indicate the correspondence of the curves to the experiments reported in Table III.

#### *Oxygen Consumption and Oxygen Pressure*

In the experiments in which worms were placed in jars containing approximately three liters of sea water, the oxygen content of the water was determined at intervals as it fell due to the metabolism of the animals. In several cases the rate of fall was accelerated by placing three worms in a jar instead of a single one. When the oxygen content had fallen to about 0.2 cc. per liter, the experiment was discontinued.

The worms were still active, as shown by persistence of spontaneous peristaltic activity.

To determine the oxygen partial pressure of the sea water, the oxygen content was plotted against time, and the oxygen content read off the curve for the middle of each period between successive samplings. Under the conditions of the experiments, namely, at a temperature of 17° C., an atmospheric pressure of 760 mm. Hg, and a sea water

TABLE III

*Oxygen Consumption and Oxygen Pressure*

Experiment and period number	Duration of period		Initial O <sub>2</sub> content	O <sub>2</sub> pressure at mid-period	Oxygen consumption
	<i>hrs.</i>	<i>min.</i>	<i>cc./l.</i>	<i>mm.Hg</i>	<i>cc./min./worm</i>
A: 1	21	30	5.15	97.6	0.0118
	2	44 00	1.78	29.0	0.0024
	3	6 30	0.28	5.6	0.0013
	4	— —	0.12	—	—
B: 1	24	00	5.19	79.0	0.0039
	2	4 10	0.42	8.5	0.0011
	3	22 00	0.18	3.9	0.0001
	4	— —	0.10	—	—
C*: 1	2	15	3.60	66.0	0.0173
	2	1 00	1.08	24.5	0.0063
	3	1 05	0.66	14.4	0.0037
	4	1 00	0.37	9.9	0.0006
	5	1 05	0.33	8.5	0.0006
	6	— —	0.28	—	—
D: 1	1	15	5.24	116.8	0.0281
	2	2 05	3.04	62.6	0.0120
	3	1 00	1.40	28.2	0.0115
	4	0 55	0.61	14.4	0.0028
	5	— —	0.42	—	—

\* At the conclusion of Experiment B, the greater part of the water was removed from the jar and fresh water substituted. The earlier parts of Experiment C then represent post-anoxybiotic metabolism, the more active oxygen consumption suggesting that an "oxygen debt" was being made up.

In Experiment A one worm was used, in the remaining experiments, three.

chloride content of 19 grams per liter, the oxygen content of water in equilibrium with atmospheric air is 5.66 cc. per liter (measured at N. T. P.). (Fox, 1907.) Under these conditions the oxygen partial pressure is 159.6 mm. Hg. The partial pressure of any sample of such water of which the oxygen content is known can be readily calculated by application of Henry's law.

To determine the rate of oxygen consumption, the change of oxygen content in any period was multiplied by the volume of water then present, due allowance being made for the volumes removed in sampling.

These data are presented in Table III and are represented graphically in Fig. 3. It is clear that, under the conditions of these experiments, the oxygen consumption of the worms decreased in an approximately linear manner with the oxygen pressure throughout the range of 116.8 to 3.9 mm. Hg. It has already been noted that the oxygen consumption of worms active in U-tubes bore no consistent relation to oxygen pressure at least over the range of 138.2 to 93.3 mm. Hg. These results are not necessarily in conflict, for (1) the ranges of pressure are not the same, overlapping by some 25 mm. Hg, and (2) the experimental conditions differed significantly.

### *Discussion*

The large literature which has accumulated relative to the influence of oxygen pressure on oxygen consumption has been most recently reviewed by Helff and Stubblefield (1931), who list the animals studied and classify their responses, and by Buchanan (1931), who gives a short historical survey of theoretical interpretations of the relationship.

Various reasons have been given for the fall of oxygen consumption which accompanies a decrease in oxygen pressure below a critical value. The applicability of these suggestions to the respiratory mechanism of *Urechis* will be discussed:

(1) *Oxygen deficiency in metabolizing cells due to inadequate transport of oxygen to them.* Accepting the doctrine of Pflüger (1872) that the oxygen consumption rate of cells is determined by their own organization and is independent of the concentration of oxygen in their immediate milieu, provided that the latter be above zero, Krogh (1916) concluded that the decline in oxygen consumption with decreasing oxygen pressure of the external medium was due to the attainment by successive groups of cells of an oxygen-free state, with consequent cessation of metabolism. This condition might result either from the absence of adequate respiratory and circulatory mechanisms, or from relatively slow diffusion of oxygen into the region of active oxidation. This conclusion has been questioned by, among others, Gerard (1931), who has shown by careful mathematical analysis of the interrelations between the oxygen consumption rate, pressure and diffusion rate in the case of unicellular organisms that Pflüger's assumption is incompatible with experimental results. He concludes that oxygen consumption must change with oxygen pressure over a significant range in that

region where the oxidation is actually taking place. Factors such as alteration of permeability to oxygen or change in concentration of oxidative enzymes (Buchanan, 1931), or decreased adsorption of oxygen on catalysts of biological oxidation (Shoup, 1929) have been suggested as possible mechanisms.

In *Urechis*, the respiratory and circulatory mechanisms, which have been quantitatively analyzed by Redfield and Florkin (1931), are quite effective, and possess large "factors of safety." The current of water through the burrow carries about six times as much oxygen as is used in metabolism. Only one-third of the oxygen taken into the hind-gut is utilized. The attainment of equilibrium between hind-gut water and blood, and between blood and active tissues, is facilitated by the peristaltic movement of both hind-gut and body-wall. The maximum distance from blood to muscle rarely exceeds one millimeter. The rate of metabolism is such that only one-sixtieth of the blood oxygen content is used per minute. The hemoglobin, fully saturated at the normal physiological oxygen pressure, becomes an oxygen transporter at lower oxygen pressures. From these considerations it seems justifiable to conclude that deficient oxygen transport to the active cells is not responsible for the fall in oxygen consumption with falling oxygen pressure in the sea water provided to the animal.

(2) *Accumulation of carbon dioxide* might decrease oxygen consumption, either of itself or by increasing the hydrogen ion concentration. In Experiment D, the three worms decreased the oxygen content of the 2664 cc. of sea water by 11.0 cc. at the end of 4.35 hours, by which time the oxygen pressure was 14.4 mm. and the oxygen consumption reduced to 10 per cent of its initial value. Assuming an R. Q. of 1, 11.0 cc. of carbon dioxide would be formed, which, in the volume of 2664 cc., would increase the carbon dioxide concentration by 0.00017 M. From the data of McClendon (1917), it may be estimated that this, in normal sea water, would cause an alteration of 0.05 mm. Hg in carbon dioxide pressure, and a pH decrease of 0.07.

Moderate increases in CO<sub>2</sub> pressure in the case of sea urchin eggs (Warburg, 1910), the lobster *Homarus americanus* and the sand worm *Nereis virens* (Amberson, Mayerson and Scott, 1924), and certain aquatic insects (Hiestand, 1931) did not decrease oxygen consumption. Root (1930) found in fertilized *Arbacia* eggs that each 10 mm. Hg of CO<sub>2</sub> pressure reduced oxygen consumption by 21 per cent. It is obvious that the change produced by 0.05 mm. CO<sub>2</sub> pressure would be negligible. Although Burfield (1928), using plaice eggs, and Fowler (1931), using *Daphnia*, found that CO<sub>2</sub> depresses oxygen consumption, their experiments are not described in a manner permitting evaluation of the small change under consideration here.

It seems improbable that accumulation of carbon dioxide was a major factor in the depression of oxygen consumption observed in *Urechis*.<sup>2</sup>

(3) *Alteration in the intensity of muscular activity.* No careful studies of the relation of the degree of spontaneous muscular activity to the oxygen pressure of the external environment have been found in the literature, although the necessity of controlling this factor is well recognized. Attempts to remove its influence by anesthesia (Gaarder, 1918; F. G. Hall, 1929) introduce new complexities, as the anesthetic used, ethyl urethane, is known to depress basic metabolism (Field and Field, 1931).

As has already been stated, reduction to 70 mm. Hg of the oxygen pressure of the water supplied to *Urechis* in U-tubes produced consistent changes in neither the degree of muscular activity nor the oxygen consumption. On the contrary, the oxygen consumption did tend to vary with the muscular activity. In this case, any influence which lowered oxygen pressure may have had upon oxygen consumption was overshadowed by the influence of muscular work. It is possible that, had lower oxygen pressures been employed, an influence of this factor might have been uncovered.

Unfortunately, no quantitative observations of the muscular activity of the worms in jars were possible.

(4) *Alteration in character of metabolism.* It is possible that the exothermic processes yielding energy for basic and functional metabolism, such as the decomposition of glycogen with the formation of lactic acid, might proceed throughout the period at a relatively constant rate, while the reconstitutive processes, which are directly or indirectly dependent on oxidations involving molecular oxygen, might lag behind, with the consequent accumulation of an "oxygen debt." In a single experiment Table III, (Experiment C) some evidence of the occurrence of such a process was obtained.

From the facts considered above it does not seem legitimate to draw any positive conclusions as to the reason for the depression of oxygen consumption accompanying the decreased oxygen content of the water. The rôle of muscular activity and of the qualitative aspect of metabolism merit further investigation.

<sup>2</sup> Since Redfield and Florkin (1931) have shown that the oxygen dissociation curve of *Urechis* hemoglobin is not influenced by the carbon dioxide pressure, criticism, such as Keys (1930) has urged against the work of F. G. Hall (1929) and others on the grounds that carbon dioxide would interfere with oxygen transport, is inapplicable to the present investigation.

## SUMMARY

The greater part of the muscular activity of the echiuroid worm *Urechis caupo* is involved in pumping a current of water through its U-shaped burrow. The magnitude of this current was studied in artificial burrows, food-free water being supplied to the animals. When the animal is not feeding, the current amounts to about eleven cubic centimeters per minute. During feeding periods, the rate of pumping rises to about twenty-nine cubic centimeters per minute. The frequency, duration and course of activity during these feeding periods has been studied. The significance of the stream in relation to provision of oxygen and food is discussed.

The oxygen consumption of the animals in U-tubes amounts to 0.00021 cc. per gram per minute, being comparable to that of related forms. It is independent of the oxygen pressure down to a value of 70 mm. Hg.

The oxygen consumption of the worms when placed in covered jars decreases with falling oxygen pressure throughout the range investigated, 115 to 4 mm. Hg. The reasons for this fall are discussed.

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